

# Unconscious processing dissociates along categorical lines

Jorge Almeida<sup>\*†‡</sup>, Bradford Z. Mahon<sup>\*§</sup>, Ken Nakayama<sup>†</sup>, and Alfonso Caramazza<sup>\*§</sup>

<sup>\*</sup>Cognitive Neuropsychology Laboratory and <sup>†</sup>Vision Sciences Laboratory, Harvard University, Cambridge, MA 02138; and <sup>§</sup>Center for Mind/Brain Sciences, University of Trento, 38068 Rovereto, Italy

Edited by Edward E. Smith, Columbia University, New York, NY, and approved August 12, 2008 (received for review June 18, 2008)

**Visual object recognition is subserved by ventral temporal and occipital regions of the brain. Regions comprising the dorsal visual pathway have not been considered relevant for object recognition, despite strong categorical biases for tool-related information in those regions. Here, we show that dorsal stream processes influence object categorization. We used two techniques to render prime pictures invisible: continuous flash suppression (CFS), which obliterates input into ventral temporal regions, but leaves dorsal stream processes largely unaffected, and backward masking (BM), which allows suppressed information to reach both ventral and dorsal stream structures. Categorically congruent primes suppressed under CFS facilitate categorization of tools but have no effect on nonmanipulable objects; in contrast, primes rendered invisible through BM facilitate target categorization for both tools and nonmanipulable things. Our findings demonstrate that information computed by the dorsal stream is used in object categorization, but only for a category of manipulable objects.**

binocular rivalry | continuous flash suppression | dorsal stream | object categorization | tools

**V**isual object recognition is subserved by the ventral visual pathway, which projects from V1 through ventral temporal and occipital structures to anterior temporal cortex (1–4). The spatial and visuomotor analyses necessary for grasping and manipulating objects are subserved by the dorsal visual pathway, which projects from V1 through dorsal occipital to posterior parietal structures (1, 5–12). The respective autonomy of the computations mediated by the ventral and dorsal streams is well established. For instance, patients with lesions to ventral stream structures may present with visual object agnosia but normal object grasping; in contrast, patients with lesions to dorsal stream structures may present with impaired object grasping and/or manipulation, but intact visual object recognition (1, 9, 12–14). It is also known that regions within the dorsal stream that are involved in object directed action show neural specificity for manipulable objects (7, 15, 16). However, regions comprising the dorsal visual pathway have not been considered relevant for object recognition, despite those strong categorical biases. Here, we show that dorsal stream computations influence object categorization processes, albeit in a highly categorical fashion (i.e., only for objects, like tools, that are manipulable).

CFS (17, 18), an interocular suppression technique, provides a direct means for testing whether computations mediated by the dorsal stream influence object recognition. It is known that posterior parietal/dorsal occipital regions show greater activation for tool stimuli compared with face stimuli when those stimuli are rendered invisible with CFS, whereas category-specific neural responses within the ventral stream to the same stimuli are obliterated (18; see also, 19–22). In experiments 1–5, we used this property of the CFS paradigm to demonstrate that information processed by the dorsal stream influences, online, the overt retrieval of semantic knowledge about tools but not nonmanipulable things. In contrast to CFS, stimuli rendered invisible through backward masking (BM) continue to activate regions within the ventral object processing stream (23), and

induce priming effects for a range of different semantic categories (24, 25). In experiment 6, we used this property of BM to show that the same categorically congruent primes used in the CFS experiments facilitate categorization responses for both tool and animal targets.

## Results

**Category Specific Priming Effects under CFS.** In experiments 1 and 2, participants indicated whether a visible target picture was a tool or an animal by means of a manual button response. Each target stimulus (tool or animal) was preceded by a prime stimulus (duration, 200 ms), that could be either congruent (same category as the target) or incongruent (different category as the target stimulus). Prime stimuli were rendered invisible using CFS by presenting the prime to only one eye, and a dynamic (10hz) random noise pattern to the other eye (Figs. 1 and 2). To avoid low-level visual priming effects, prime and target stimuli (throughout all experiments) were never the same basic level items (see *Methods* for details). Participants were unaware of both the presence and identity of the primes, as demonstrated by the percentage correct performance of participants in detection (experiment 1) and discrimination tasks (experiment 2) carried out over the prime stimuli [See Table 1, [supporting information \(SI\) Fig. S1 a and b](#), and *Methods* for details].

Analyses of response times to the target pictures in experiment 1 showed that the categorization responses of participants were facilitated by categorically congruent suppressed primes [ $F(1,30) = 5.90$ ;  $P < 0.02$ ; and  $\eta^2 = 0.164$ ; Fig. 3]. Planned comparisons showed that this priming effect was modulated by the category of the target. Participants were faster to categorize a tool when tool primes were presented than when animal primes were presented [ $t(31) = 3.44$  and  $P < 0.002$ ; priming effects ranged from  $-29$  to  $104$  ms; mean,  $18$  ms; SEM,  $5$  ms) but there was no effect for animal targets ( $t < 1$ ; mean priming effect,  $3$  ms; SEM,  $5$  ms).

Experiment 2 followed the same protocol as experiment 1, except that a discrimination task over the primes was used as an index of successful suppression of the prime stimuli (i.e., participants had to decide whether a prime was a tool or an animal; see Table 1). The reason for using a discrimination task in experiment 2 (as opposed to a detection task in experiment 1) was to obtain a more stringent measurement of the information that is available from a suppressed stimulus for making a categorization decision. In addition, a different set of animal and tool stimuli was used as primes and targets (see *Methods* for details). As in experiment 1, the same pattern of semantic priming modulated by the category of the target pictures was

Author contributions: J.A., B.Z.M., K.N., and A.C. designed research; J.A. performed research; J.A. analyzed data; and J.A., B.Z.M., K.N., and A.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

<sup>†</sup>To whom correspondence should be addressed. E-mail: jalmeida@wjh.harvard.edu.

This article contains supporting information online at [www.pnas.org/cgi/content/full/0805867105/DCSupplemental](http://www.pnas.org/cgi/content/full/0805867105/DCSupplemental).

© 2008 by The National Academy of Sciences of the USA







CFS, or interocular suppression techniques more generally (26–28). Previous attempts to obtain high-level priming effects with interocular suppression techniques may have failed because they did not distinguish between stimuli that do (i.e., tools) and do not (i.e., animals, vehicles) have strong representations in the dorsal object processing stream. In Fig. 3, we summarize the results of experiments 1–6: categorically congruent primes rendered invisible through CFS facilitated categorization responses for tool but not animal or vehicle targets, when compared with categorically incongruent primes. These results are robust across different stimuli, measures of prime awareness (detection vs. discrimination), modality of response (manual vs. vocal), target format (picture vs. written word), and semantic category contrasts (tools vs. animals and tools vs. vehicles). In contrast, the same categorically congruent primes rendered invisible through BM facilitated categorization responses for both animal and tool targets.

The overall pattern of results indicates that semantic priming effects are modulated by interactions between the content of the stimulus and the computations that it engenders. Specifically, the dimension of “being a manipulable object” seems to be critical for priming effects to be induced by CFS suppressed stimuli. The pattern of results obtained suggests that dorsal stream computations mediating object directed action influence object recognition processes for manipulable objects.

An important issue that is raised by the findings that we have reported concerns the nature of the information that is processed by dorsal stream structures, and which ultimately affects object recognition processes. The tool stimuli that were used in these experiments all had an elongated principal axis. Thus, one issue that arises is whether similar effects would be observed for manipulable/graspable objects that do not share this visuo-motor characteristic (see ref. 15 for discussion). More generally, our findings raise questions about whether dorsal stream structures represent detailed and “abstract” knowledge about visually presented objects. For instance, it could be argued that the information computed by the dorsal stream that is relevant for observing priming from CFS stimuli is relatively abstract and concerns the category membership of the stimulus. However, as discussed above, neuropsychological evidence indicates that patients with lesions to ventral occipital-temporal regions can have profound difficulties naming objects, but unimpaired visuo-motor abilities with the same objects (e.g., patient DF; 1). Those data place an important upper boundary on what the dorsal stream can be assumed to represent about an object, at least as that information is explicitly available to individuals/patients. Nevertheless, our findings, and the experimental paradigm we have presented, offer a previously undescribed way of studying these issues in the normally functioning and intact brain.

Whereas there is a range of evidence (both behavioral and physiological) with human and nonhuman primates demonstrating that binocularly suppressed stimuli have different effects on ventral and dorsal stream structures (18, 19–22), much remains unknown about how information reaches dorsal stream structures. One possibility is that information reaches the dorsal processing stream through subcortical routes (18, 20). An important possibility opened up by our findings is that information arriving through subcortical structures is filtered along lines that map onto conceptual categories. Consistent with this hypothesis, Pasley *et al.* (20) found that suppressed emotional faces activated the amygdala, and that the provenance of this activation could be traced to the superior colliculus. Of particular relevance to the present study is the fact that regions within the posterior parietal cortex are the target of projections from the superior colliculus (29). Another possibility is that stimuli are not filtered along categorical lines within subcortical structures, but are rather sorted based on the response preferences of the cortical regions that receive subcortical input.

Our findings also indicate that there is more than one way in which an object may be invisible. By rendering stimuli invisible with CFS and BM, we took advantage of the different kinds of information that became available to cognitive systems in each technique. We believe that these differences in the availability of information are responsible for the dramatic disparity in subsequent behavior, including high-level decisions, observed in our experiments. Along the lines of the distinction advanced by Dehaene *et al.* (30) between unconscious and preconscious processes, it is possible to distinguish different types of unconscious processes according to the pathways that information takes from the eye to the cortex.

## Methods

**Participants and Apparatus.** For this study, 114 Harvard University undergraduate students participated in the experiments in exchange for course credit or payment (32 participated in experiment 1, 13 in experiment 2, 11 in experiment 3, 30 in experiment 4, 20 in experiment 5, and 8 in experiment 6). All participants had normal, or corrected to normal vision and gave written informed consent. The project was approved by the Committee for the Use of Human Subjects at Harvard University. All participants were right handed (Edinburgh Handedness questionnaire), and were naïve as to the experimental hypotheses.

All experiments were run on a Dell PC, with a ViewSonic ultrabrite A90+ monitor. The monitor refresh rate was 100 Hz for experiments 1–5 and 85 Hz for experiment 6. Stimulus presentation was controlled by DMDX (31). The tool and animal pictures that were used in the experiments have been described elsewhere (15). The vehicle pictures were obtained from the internet.

**Continuous Flash Suppression.** For experiment 1, 10 pictures were selected as experimental stimuli, five animals and five tools (as defined in ref. 15). For each category, one of the pictures was selected as a prime, whereas the others were used as targets. For experiments 2–3, 16 pictures were selected as experimental stimuli (eight animals and eight tools). In experiment 5, we used the same tool pictures, and we selected eight pictures of vehicles as experimental stimuli, replacing the animal pictures. For each category, half of the items were selected to be targets, whereas the other half was selected as primes. Care was taken so that the selected primes for experiments 2, 3, and 5 were not used as primes in experiment 1, and the targets were not used as targets in experiment 1. The stimuli were presented centrally, and subtended  $\approx 7^\circ$  of visual angle; 70% additive noise was added to the target stimuli by using Photoshop, to avoid ceiling performance. For experiment 4, the words corresponding to the picture targets used in experiment 2 were used as targets, whereas the same prime pictures were used as in experiments 2–3. Participants were seated comfortably, and at a distance of  $\approx 50$  cm from the screen.

Experiment 1 was run by using four levels of contrast for the primes, whereas experiments 2–5 were run by using three levels of contrast for the primes. For experiments 1–5, there were four targets per category that were presented with either one (experiment 1) or four categorically congruent primes (experiments 2–5), and one or four categorically incongruent primes. These stimuli assignments were repeated 10 times in experiment 1, for a total of 160 trials per contrast level (640 total trials), and three times in experiments 2–5, for a total of 192 trials per contrast level (576 total trials).

For experiments 1–5, the contrast of the prime pictures was adjusted for each participant so that prime invisibility was successfully achieved. Percentage correct performance of participants on the prime detection or discrimination task was used to select, offline, the particular contrast level for the main analysis of the experiment proper. For all experiments, the highest level of contrast for which the performance of participants was not above chance, as defined by a *z* test for one proportion (exp. 1–5), and for which discrimination was not different between the two categories, as determined by a *z* test for two proportions (experiments 2–5), was selected for the main analysis. The data for participants whose performance in the detection or discrimination tasks did not meet specified criteria for inclusion for any of the contrast levels of the prime stimuli were discarded.

For experiments 1–5, after completing the experiment, participants performed a prime detection (experiment 1) or discrimination task (experiments 2–5) by using the same contrast levels that were used during the experiment (Table 1). In the detection task after experiment 1, the two primes (one animal, one tool) were repeated 12 times; 24 random patterns without prime pictures were used as noise alone trials. This trial set was repeated for each contrast level. Participants were asked to indicate if they detected something other than the noise patterns. In experiments 2–5, each prime was repeated 10

times, for a total of 80 trials per contrast level. Participants were asked to categorize, to the best of their ability, the primes as animals or tools.

**BM.** Experiment 6 used the same stimuli as experiment 2. We added 70% additive noise to the prime stimuli by using Photoshop to facilitate masking. A black and white backward mask was generated, by using the same algorithm that was used to generate the high-contrast random noise patterns for CF5. Experiment 6 followed the same design as experiments 2. The discrimination task was the same as that used in experiments 2–5, as well as the criteria for prime invisibility.

**Analyses.** For all six experiments, a 2 (Target Category, animals vs. tools) X 2 (Prime Category, animals vs. tools) ANOVA was performed. The *F* values for the

interaction between these two factors are reported. Planned comparisons were performed over the two-way interaction between target category and prime category, for each target category.

**ACKNOWLEDGMENTS.** We thank Petra Pajtas and Lukas Strnad for their help collecting data; Fang Fang and Bruno Breitmeyer for their advice on the experimental design; and M. Clara Barata and Petra Pajtas for their comments on earlier versions of this manuscript. A.C. was supported by National Institute on Deafness and other Communication Disorders Grant R01 DC006842 and by the Fondazione Cassa di Risparmio di Trento e Rovereto. J.A. was supported by Fundação para a Ciência e a Tecnologia, Portugal Grant SFRH/BD/28994/2006. B.Z.M. was supported by a National Science Foundation Graduate Research Fellowship. K.N. was supported by National Institutes of Health Grant HSD-DHB-MOD 0433136/0433226.

- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15:20–25.
- Chao LL, Haxby JV, Martin A (1999) Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat Neurosci* 2:913–919.
- Kanwisher N, McDermott J, Chun MM (1997) The fusiform face area: A module in human extrastriate cortex specialized for face perception. *J Neurosci* 17:4302–4311.
- Noppeney U, Price CJ, Penny WD, Friston KJ (2006) Two distinct neural mechanisms for category-selective responses. *Cerebral Cortex* 16:437–445.
- Ungerleider LG, Mishkin M (1982) *Analysis of Visual Behavior*, eds Ingle DJ, Goodale MA, Mansfield RJW (The MIT Press, Cambridge, Mass), pp 549–586.
- Murata A, Gallese V, Luppino G, Kaseda M, Sakata H (2000) Selectivity for the shape, size and orientation of objects for grasping in neurons of monkey parietal area AIP. *J Neurophysiol* 83:2580–2601.
- Johnson-Frey SH, Newman-Norlund R, Grafton ST (2005) A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral Cortex* 15:681–695.
- Johnson-Frey SH (2004) The neural bases of complex tool use in humans. *Trends Cogn Sci* 8:71–78.
- Jeannerod M, Decety J, Michel F (1994) Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia* 32:369–380.
- Jeannerod M, Arbib MA, Rizzolatti G, Sakata H (1995) Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends Neurosci* 18:314–320.
- Culham J, et al. (2003) Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Exp Brain Res* 153:180–189.
- Carey DP, Harvey M, Milner AD (1996) Visuomotor sensitivity for shape and orientation in a patient with visual form agnosia. *Neuropsychologia* 34:329–337.
- Ochipa C, Rothi LJ, Heilman KM (1989) Ideational apraxia: A deficit in tool selection and use. *Ann Neurol* 25:190–193.
- Mahon BZ, Caramazza A (2005) The orchestration of the sensory-motor systems: Clues from neuropsychology. *Cognitive Neuropsych* 22:480–494.
- Mahon BZ, et al. (2007) Action-related properties shape object representations in the ventral stream. *Neuron* 55:507–520.
- Chao LL, Martin A (2000) Representation of manipulable man-made objects in the dorsal stream. *NeuroImage* 12:478–484.
- Tsuchiya N, Koch C (2005) Continuous flash suppression reduces negative afterimages. *Nat Neurosci* 8:1096–1101.
- Fang F, He S (2005) Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nat Neurosci* 8:1380–1385.
- Kreiman G, Fried I, Koch C (2002) Single-neuron correlates of subjective vision in the human medial temporal lobe. *Proc Natl Acad Sci USA* 99:8378–8383.
- Pasley BN, Mayes LC, Schultz RT (2004) Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron* 42:163–172.
- Sheinberg DL, Logothetis NK (1997) The role of temporal cortical areas in perceptual organization. *Proc Natl Acad Sci USA* 94:3408–3413.
- Tong F, Nakayama K, Vaughan JT, Kanwisher N (1998) Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21:753–759.
- Dehaene S, et al. (2001) Cerebral mechanisms of word masking and unconscious repetition priming. *Nat Neurosci* 4:752–758.
- Breitmeyer BG, Ogmen H (2000) Recent models and findings in visual backward masking: A comparison, review, and update. *Percept Psychophys* 62:1572–1595.
- Finkbeiner M, Caramazza A (2008) Modulating the masked congruence priming effect with the hands and the mouth. *J Exp Psychol Hum Percept Perform*, 34:894–918.
- Zimba LD, Blake R (1983) Binocular rivalry and semantic processing: Out of sight, out of mind. *J Exp Psychol Hum Percept Perform* 9:807–815.
- Cave CB, Blake R, McNamara TP (1998) Binocular rivalry disrupts visual priming. *Psychol Sci* 9:299–302.
- Blake R, Logothetis NK (2002) Visual competition. *Nat Rev Neurosci* 3:13–21.
- Clower DM, West RA, Lynch JC, Strick PL (2001) The inferior parietal lobule is the target of output from the superior colliculus, hippocampus, and cerebellum. *J Neurosci* 21:6283–6291.
- Dehaene S, Changeux J-P, Naccache L, Sackur Jrm, Sergent C (2006) Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends Cogn Sci* 10:204–211.
- Forster KI, Forster JC (2003) DMDX: A Windows display program with millisecond accuracy. *Behav Res Meth Ins C* 35:116–124.